Observations on the Anatomy and Biology of Two California Vermetid Gastropods

BY

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(Plate 45; 4 Text figures)

INTRODUCTION

THE MARINE GASTROPODS included in the family Vermetidae form a morphologically distinct group characterized by shells which are uncoiled and cemented to a substratum. This feature is shared with the prosobranchs of the family Siliquariidae to which the Vermetidae are closely related. The siliquariids are distinct from the vermetids in having a long slit through the mantle wall and shell on the right side beneath the rectum, and in retaining a spiral corkscrew shape in their shell (Morton, 1951, 1955). Both families are placed in the mesogastropod super-family Cerithiacea, which contains, in addition, such well known temperate forms as Turritella, Cerithium, and Bittium (THIELE, 1931; Morton, 1958).

There have been very few comprehensive treatments of the vermetids. Between 1900 and 1940 only 3 papers appeared which were devoted to aspects of the biology of vermetids (though taxonomic citations occur in other works); these were Boettger (1930), Yonge (1932), and Yonge & Iles (1939). Boettger was concerned with nutritional physiology, while Yonge & Iles compared certain points of the anatomy of Serpulorbis gigas (BIVONA-BERNARDI, 1832) of the Mediterranean with that of Dendropoma maximum (Sowerby, 1835) from Australia.

Since 1940 the vermetids have received considerable attention at the hands of Professor J. E. Morton of Auckland (1950; 1951, a, b, c; 1955; 1965). It was Morton who separated the vermetids and siliquariids into two taxa (1951) and attempted to establish sound anatomical criteria for the generic groupings within the Vermetidae (1965). Keen (1961) had already performed the exceedingly difficult task of reducing the more than 45 nominal genera to a realistic 5.

Morton has been particularly interested in mechanisms of feeding in the vermetids and in the evolution of the group. While he did have access to preserved material of *Petaloconchus montereyensis* (Dall, 1919) and *Serpulorbis squamigerus* (Carpenter, 1857), the species studied here, Morton's discussion of function in these species is based upon inferences from anatomy. Morton's descriptions of the digestive system are complete, but he has only briefly described the reproductive system and has omitted reference to the nervous system altogether.

Compared with that for most other large prosobranch families, our knowledge of the biology of living vermetids is slight, and concerns only a small number of species. Of some 250 nominal species of Vermetidae, only 8 or 9 have been examined alive. Morton (1965) discussed most of the literature on this topic and the only subsequent work is a study by URIEL SAFRIEL (1966) on the "vermetid formations" of the Israeli shore of the Mediterranean Sea in which he presents an interesting description of the geological effects of vermetid intertidal zonation.

The following discussion of anatomy and biology of the two California vermetid species, *Petaloconchus montereyensis* and *Serpulorbis squamigerus*, provides a background for detailed information on reproduction to be discussed in subsequent papers, and presents certain new information on systems in these species for which published accounts are lacking.

MATERIALS AND METHODS

Serpulorbis squamigerus (CARPENTER, 1857)

While a few specimens of this species were collected on the Monterey Peninsula, most of the animals used were taken at Malibu and Newport Beach, California. For the sake of comparison, animals were also collected at San Diego, La Jolla, Newport Bay, and Santa Barbara, California. The animals collected at these localities, though differing in their habitats, were all clearly of one species.

Petaloconchus montereyensis (DALL, 1919)

Most of the animals utilized in this study were collected from two restricted populations on Mussel Point adjacent to the Hopkins Marine Station, Pacific Grove, California. Other specimens, taken for comparative purposes, were collected at Point Pinos and Pescadero Point, on the Monterey Peninsula.

Both species were kept for periods of up to more than one year at 12° to 16° C in aquaria at Hopkins Marine Station. The aquaria were provided with a continuous flow of fresh seawater pumped from Monterey Bay. While the animals survived well in the laboratory, they usually ceased reproductivity within one to two weeks after their confinement in aquaria. Except in feeding experiments, no attempt was made to provide food for the animals other than the plankton which passes through the filters at the seawater intake.

The living animals were examined both grossly and microscopically in small dishes of seawater under a dissecting microscope. It was necessary to anesthetize animals before removing them from their shells for observation and dissection. Anesthetization was brought about by immersing the animals in an aqueous solution of magnesium chloride isotonic to sea water (75 g per 1 l of tap water). The animals were usually completely immobilized by this treatment in 3 to 4 hours.

ANATOMY

Serpulorbis squamigerus and Petaloconchus montereyensis, like all the members of the family Vermetidae, construct calcareous shells which are securely cemented to a substratum. While the configuration of these shells (see Keen, 1961) is unlike that of most gastropods, the animals themselves possess fairly typical gastropodan bodies which may be divided into head-foot, pallial, and abdominal regions (Text figure 1; Plate 45, Figures 3, 4).

The foot is cylindrical, naked in Serpulorbis but covered by an operculum in Petaloconchus (Text figure 4A; Plate 45, Figure 2). The muscular mass of the foot is directly connected with the well-developed columellar muscle which runs up the ventral side of the pallial region. Since the major portion of the adult foot bears the operculum in most vermetids, this part of the foot is considered to correspond to the metapodium of the foot of the vermetid juvenile and other free-living snails (see Morton, 1955). The mesopodium is represented in the adult vermetid by a small shield-shaped pad of tissue below the mouth,

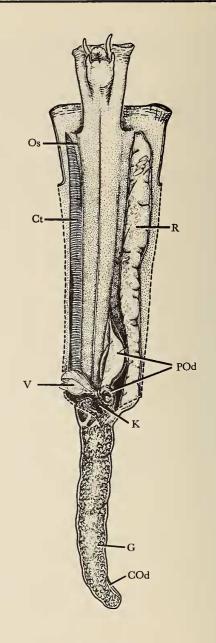


Figure 1

Female Serpulorbis squamigerus with the mantle wall opened along the dorsal mid-line and deflected to show pallial structures.

Ct - ctenidium; K - kidney; G - ovary; Os - osphradium; POd - pallial oviduct R - rectum V - ventricle

while the orifices of the large pedal mucus glands and the pedal tentacles together represent the propodium. The two pedal tentacles, which originate in depressions ventrolateral to the mouth, are very extensible, and each has a groove running up its mesial margin. The snout, with the horizontal slit-shaped mouth at its terminus, is directly above the propodium. Slightly posterior to the snout, on each side of the dorsal surface of the head, a cephalic tentacle arises; each bears an eye on its posterior lateral margin. The head narrows behind the eyes to form a "neck" region at the entrance to the mantle cavity.

In life, the head and foot of both species are mostly black with small amounts of orange pigmentation around the foot and the lateral ridges of the head. However, the color pattern of *Petaloconchus montereyensis* is quite variable, and in some populations the predominant ground color of the head is brownish-orange. The thickened edge of the mantle which encircles the head and foot is brownish-orange with flecks of dense white.

The mantle cavity is relatively deep, extending for 50% of the total length of the animal in Serpulorbis and 40% in Petaloconchus. The roof of the cavity displays the only strongly sexually dimorphic character in Serpulorbis. Here, in reproductively active females, a long slit in the median dorsal mantle wall provides contact between the mantle cavity and the shell over the pallial region (Plate 45, Figure 4). The egg capsules are attached to the exposed shell in this region. No such slit occurs in the females of Petaloconchus.

A ridge of muscular tissue arises on the posterior dorsal surface of the head and runs posteriorly, dividing the ventral portion of the mantle cavity into right and left halves (Text figure 2A). The ridge flattens out only in the most posterior portion of the pallial cavity. The organs lying within the mantle cavity are those of a typical prosobranch mesogastropod (Text figure 1). They include an elongate ctenidium on the left wall composed of triangular lamellae, a long osphradium lying beneath the gill, a hypobranchial gland on the mantle cavity roof, the rectum on the right dorsal portion of the roof, pallial reproductive structures in the posterior right ventral region.

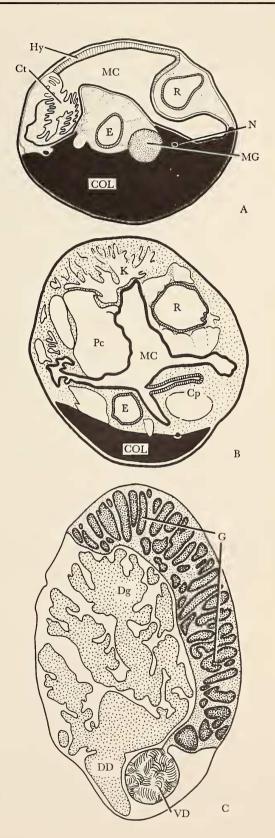
Figure 2

(adjacent column →)

Diagrammatic cross-sections through Serpulorbis squamigerus

A: through the anterior portion of the mantle cavity of a female;
B: through the posterior portion of the mantle cavity;
C: through the abdominal region of a sexually mature male.

DD - digestive gland duct; COL - columellar muscle;
Cp - capsule gland; Ct - ctenidium; Dg - digestive gland;
E -esophagus; G - gonad; Hy - hypobranchial gland;
K - glandular portion of kidney; MC - mantle cavity;
MG - pedal mucous gland; Pc - pericardium R - rectum
N - right pleuro-visceral nervous connective; VD - vas deferens



and the kidney orifice in the posterior wall (Text figures 1, 2A, 2B). The kidney consists of a large sac placed directly behind the mantle cavity on the right half of the body, and a large amount of excretory tissue which extends out into the posterior roof of the mantle cavity (Text figure 2B). On the left side the pericardium extends dorsally and anteriorly over the more posterior part of the pallial cavity (Text figure 2B). It contains the large ventricle and the smaller auricle of the heart.

The mouth opens into a buccal cavity surrounded by a massive buccal muscular apparatus which manipulates the jaws and radula. The buccal cavity opens dorsally into the esophagus which is provided with a pair of salivary glands borne on the posterior dorsal surface of the buccal mass. The esophagus is very long and runs from the buccal mass directly posteriorly beneath the mantle cavity, the heart, and the kidney, to the stomach. The large pedal mucous glands lie parallel to the esophagus along half its length (Text figure 2A).

Behind the heart and kidney lies the abdominal region of the body. The anterior portion of this region contains several coils of the intestine, the stomach, and the style sac. Behind the stomach is a tail-like region of variable length which contains the digestive gland on the left and the gonad on the right (Text figure 2C). The major channel of the digestive gland is ventral in position, as are the major blood lacunae, the abdominal nervous extensions, and the gonoduct.

The elongate columellar muscle originates in the foot, forms the ventral portion of the body mass in the pallial region, emerges from the body at the level of the posterior end of the pallial cavity, and continues backward as a long free strap to its insertion far back inside the shell.

The nervous system of vermetid gastropods has been examined only in Vermetus triqueter (BIVONA-BERNARDI, 1832) by LACAZE-DUTHIERS, 1860. The ganglia and major nerves of Serpulorbis squamigerus are easily examined after anesthetization and formalin fixation of the animal. The details of the nervous system of this species are presented in Text figure 3. All major ganglia are paired, a condition generally accepted as primitive in gastropods (Fretter & Graham, 1962), and all except the parietal (or supra- and sub-esophageal) ganglia lie in their expected complementary bilateral positions. The sub-esophageal ganglion is located next to the posterior face of the left pleural ganglion. The supra-esophageal ganglion is well removed from the circumesophageal nervous complex; it lies more posteriorly and to the left, near the osphradium.

The cerebral ganglia lie on the esophagus posterior to the buccal mass. They are provided with thick connectives to the pleural and pedal ganglia and are linked across the esophagus by a thick cerebral commissure. Three large nerve trunks leave each cerebral ganglion anteriorly. The most lateral of these bifurcates, one nerve going to the region of the mouth and the other recurving and penetrating the buccal mass to connect with the buccal ganglion on that side. The buccal ganglia lie on the posterior dorsal face of the buccal mass, and innervate the complex musculature of the buccal apparatus. The middle nerve arising from each cerebral ganglion runs to the lips and the innermost nerve innervates the eye and cephalic tentacle on its side.

The pleural ganglia lie ventrally to the cerebral ganglia with which they are connected by thick commissures. A commissure also links each pleural with the pedal ganglion of the same side. The left pleural ganglion is closely associated with the sub-esophageal ganglion. A nerve arises from the dorsal face of each pleural ganglion to innervate the neck musculature on each side. From the postero-lateral face of each pleural ganglion a large nerve arises which receives a zygoneuric connection from the pleuro-visceral loop. Proximal to the point of zygoneury, the nerve arising from the left pleural ganglion sends one branch to innervate the mantle edge on the same side; distal to the zygoneuric connection from the supra-esophageal ganglion, the nerve runs on to innervate the osphradium and ctenidium. The corresponding nerve originating from the right pleural ganglion receives the zygoneuric connection from the sub-esophageal ganglion and extends toward the right side; it soon bifurcates, the larger anterior branch innervating the mantle edge, while the smaller branch runs posteriorly to the mantle wall in the region of the anus.

A third large nerve, the left segment of the pleuro-visceral loop, arises from the right pleural ganglion, runs diagonally posteriorly dorsal to the esophagus, and enters the supra-esophageal ganglion on the left side. From this ganglion arise the left zygoneury, a large osphradiobranchial nerve, and the remaining posteriorly directed left part of the pleuro-visceral loop. The right segment of the pleuro-visceral loop originates anteriorly from the sub-esophageal ganglion and runs diagonally posteriorly, beneath the esophagus.

The pedal ganglia are connected with each other by a sub-esophageal commissure and with the cerebral and pleural ganglia on their respective sides by thick connectives. From the anterior face of each pedal ganglion 3 large nerves and one slender nerve arise. The latter, which has a slightly dorsal origin, and the most lateral of the thicker nerves innervate the muscles of the basal wall of the head. The middle of the larger nerves arising from each pedal ganglion runs directly anteriorly to innervate

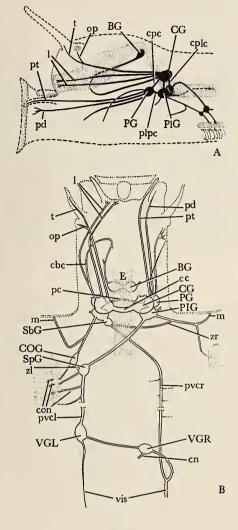


Figure 3

The nervous system of Serpulorbis squamigerus

A: lateral view of the cerebral complex B: dorsal view, pleuro-visceral connectives foreshortened

BG - buccal ganglion CG - cerebral ganglion COG - ctenidial-osphradial ganglion; PG - pedal ganglion; SbG - sug-esophageal ganglion; PIG - pleural ganglion; SpG - supra-esophageal ganglion; VGL - left visceral ganglion; E - esophagus; VGR - right visceral ganglion; cn - cardiac nerve; cbc - cerebro-buccal connective; con - ctenidial-osphradial nerves; cpc - cerebro-pleural connective; 1 - labial nerves; m - mantle nerves; op - optic nerve; pc - pedal commissure; pd - pedal nerve; pt - pedal tentacle nerve; plpc - pleuro-pedal connective; pvcr - right pleuro-visceral pvcl - left pleuro-visceral connective; vis - visceral nerves; connective; t - tentacular nerve; zr - right zygoneury zl - left zygoneury;

the foot. The medial large nerve on each side innervates the respective pedal tentacle.

The remaining portion of the nervous system consists of the posterior segment of the pleuro-visceral loop and its branches. The right side of this loop runs beneath the mantle cavity and extends small branches to the mantle wall and floor. It passes beneath the posterior wall of the mantle cavity (adjoining the anterior wall of the kidney sac) and continues posteriorly in close association with the gonoduct. Below the kidney, where the coelomic gonoduct turns dorsally to join the pallial gonoduct, the right pleuro-visceral connective branches, one branch continuing posteriorly, the other running dorsally in the kidney wall to the right visceral ganglion which lies in the anterior kidney wall directly above the origin of the pallial gonoduct. From the right visceral ganglion two nerves arise. One runs to the pericardial region; the other, forming the posterior portion of the pleuro-visceral loop, extends to the left to join the left visceral ganglion near the posterior end of the ctenidium. From the left visceral ganglion a nerve arises which runs posteriorly along the ventral surface of the animal into the abdominal region. A similar nerve, the continuation of the right pleuro-visceral connective, runs into the abdomen on the right ventral side of the animal in conjunction with the gonoduct; it appears to innervate the gonad.

The pattern of the nervous system shown here is typical for members of the super-family Cerithiacea (see BOUVIER, 1887, for numerous other examples). The major variations here are the retention of unfused visceral ganglia and the absence of statocysts which occur on the pedal ganglia of most other gastropods. Considering the sessile habit of the vermetids, the absence of statocysts is not surprising.

The nervous system of Serpulorbis squamigerus is nearly identical to that shown for Vermetus triqueter by LACAZE-DUTHIERS (1860), except that S. squamigerus has a left visceral ganglion while V. triqueter does not.

BIOLOGY

Serpulorbis squamigerus

MACGINITIE & MACGINITIE (1968) discussed the habitat, the gregarious nature, and the mucous-net mode of food collecting of these snails. Further details from the present study are added below.

The mucous nets are a product of the extensive paired pedal mucous glands. These glands are capable of secreting a net as large as 50 cm² in 3 to 4 minutes. The mucus flows out of the median aperture between the bases of the pedal tentacles and is carried distally by ciliary cur-

rents in the grooves on the pedal tentacles. The pedal tentacles thus spread the single string of mucus issuing from the aperture of the gland into a triangular sheet (Plate 45, Figure 1). Some hardening of the mucus apparently occurs on contact with seawater. The density of the mucus is close to that of seawater since the net is buoyed upward by very slight turbulence or by only a few tiny trapped bubbles.

The mucous net remains suspended in the water for 10 to 30 minutes and is then retrieved by the action of the radula and jaws. The radula is extended far out of the widely-opened mouth; it grasps the mucous net and pulls it a short distance down and into the mouth. The jaws then close on the mucus, holding it during swallowing and disengagement of the radula. The esophagus of Serpulorbis squamigerus is very long and extensible, a modification which provides a large storage area for the rapidly ingested mucous net before its slower passage into the stomach.

In laboratory aquaria individuals of Serpulorbis squamigerus may be stimulated to produce mucous nets by either strong water currents or agitation of the water. The addition of dried and ground algae or dried animal matter (commercial pet fish food) to unagitated water in the aquaria did not elicit feeding, nor did the addition of live copepods (Tigriopus californicus Baker, 1912). It would thus appear that the usual stimulus for feeding in this species is water turbulence (the incoming tide?) and not the presence of food, as Boettger (1930) found to be the case for S. gigas.

Individuals of Serpulorbis squamigerus are predominantly gregarious, but not exclusively so. They are often found widely separated from one another on floats in southern California yacht basins. In these instances the "communal mess table" emphasized by Morton (1965) does not occur, but the animals are apparently successful in their enforced solitary feeding, for isolated individuals are often of much greater size than aggregated ones.

While the mucous-net method is the predominant method of feeding in *Serpulorbis squamigerus* it may not be the only one; examination of the ciliary currents of the mantle cavity clearly shows that material filtered out of

seawater by the gills is passed to the oral region. Actual ingestion of this material was not observed.

Just what constitutes the major food of Serpulorbis in the field is still uncertain. Laboratory aquaria undoubtedly present an anomalous situation. However, examination of nets extended in the aquaria shows them invariably to contain numerous diatoms, skeletons of small crustaceans, and unidentifiable debris. In paraffin sections through the stomach region of S. squamigerus taken in the field I have seen diatoms and occasional small crustaceans and worms. Whether or not the snails are capable of digesting animal matter remains open to investigation. The presence of a crystalline style would appear to argue against such a possibility (Yonge, 1930, 1932).

MacGinitie & MacGinitie (1968) state that Serpulorbis squamigerus is preyed upon by the carnivorous prosobranchs Ceratostoma foliatum (GMELIN, 1791) and Shaskyus festivus (HINDS, 1844). In the present study no predators have been seen, but the presence of trematode cercariae in the abdomen of S. squamigerus has been noted frequently. These cercariae appear to feed exclusively on the gonad of the snail and may cause nearly total castration. An occasional commensal of S. squamigerus is a pinnotherid crab, tentatively identified as Opisthopus transversus RATHBUN, 1893. These crabs occur in the mantle cavity, and when removed from one snail have been observed to re-enter the mantle cavity of another host quite readily. The snails exhibit little response to the entrance of the crab. Curiously, this association has only been noted in snails collected from the Malibu region of California and never from animals collected to the north or south of this area. The pinnotherids were noted in individuals of S. squamigerus collected in March and May 1966.

As might be expected, the numerous spaces between the tubes of large masses of *Serpulorbis* provide refuge for great numbers of other invertebrates. Among these are calyptraeid gastropods, nemerteans, sipunculids, polychaetes, and the ubiquitous nematodes. The tips of the vermetid tubes are frequently encrusted by bryozoans, sponges, and compound ascidians.

Explanation of Plate 45

Figure 1: Serpulorbis squamigerus feeding (X 1)

Figure 2: Petaloconchus montereyensis: mass of living individuals (× 2.5)

Figure 3: Preserved specimen of Serpulorbis squamigerus seen from the right side (× 1.5)

Figure 4: Preserved specimens of Serpulorbis squamigerus, male and female, seen in dorsal view (× 1.5)

and remaie, seen in dorsal view (X 1.5)

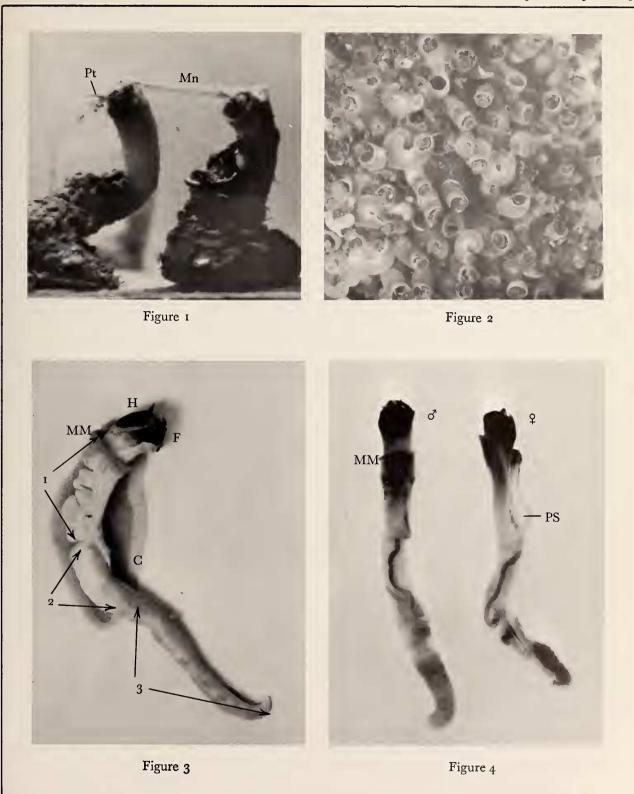
C - columellar muscle; F - foot; H - head;

MM - mantle margin; Mn - mucous net;

PS - pallial slit of female;

Pt - pedal tentacle;

1, 2, and 3 represent gross body regions: 1, mantle cavity; 2, region of heart, kidney and stomach; 3, region of digestive gland and gonad





Just how dense the populations of Serpulorbis squamigerus may be in some localities was illustrated by Peque-GNAT (1964) who reported concentrations of this species of 650 per m². The greatest concentrations of S. squamigerus seen in the present study are on a small sandstone outcropping adjacent to the beach at the Kerkhoff Marine Laboratory, Newport Bay, California. The stone is surrounded by muddy sand which limits the spread of S. squamigerus, but nearly every square inch of exposed rock is covered by them. Sponges and bryozoans are also abundant on and around the vermetid tubes.

KEEN (1961, p. 203) gives the range for Serpulorbis squamigerus "from Monterey, California, to southern Baja California." This is undoubtedly more accurate than the listing by R. T. Abbott (1954), "Forrester Island, Alaska to Peru," since many of the reports on which Abbott's range is based are by authors who confused S. squamigerus with other vermetids, some not even of this genus (Oldroyd, 1924, describes "Aletes squamigerus" as a species bearing an operculum!). Nowhere north of Point Conception, California have large numbers of S. squamigerus been seen, and on the Monterey Peninsula they are rare.

Within the range given by KEEN (1961), the vertical distribution of Serpulorbis squamigerus is poorly known. Studies on the biota around sewer outfalls and off-shore oil wells (Turner et al, 1962, 1965a, 1965b) include records of S. squamigerus from the intertidal zone to depths of 80 feet. A more reliable maximum depth is probably 50 feet, since the 80 foot record was of a single specimen (a shell?) found on a sandy bottom, an unlikely habitat for a vermetid. In the area studied by Pequegnat (1964), which consisted of two sandstone reefs offshore from Corona Del Mar, California, S. squamigerus was noted to occur on the reef tops, average depth 11 m, in areas of greatest turbulence.

Petaloconchus montereyensis

Petaloconchus montereyensis is known only from conchological faunal lists and Morton's (1965) partial description of the animal based on preserved material. Specimens used in this study were collected from the type locality, "Monterey, California" (Dall, 1919), and the surrounding coast.

Morton (op. cit.) has suggested that Petaloconchus montereyensis should be capable of both ciliary filter feeding and feeding with mucous nets (his judgments were based on relative size of the ctenidium and pedal mucous glands). This is indeed the case. The ciliary and glandular tracts of the gill and mantle walls carry particles from the gills forward over the mantle floor to the mesopodial pad in front of the mouth where they are mixed with mucus and then ingested. However, the predominant method of feeding is by means of mucous nets

as in Serpulorbis squamigerus. The nets of Petaloconchus are fragile, and in aggregates of these snails they are fused in a thin veil which overlies a whole portion of the colony. The nets are so thin as to be barely discernible unless they are laden with detritus particles. The nets are produced and retrieved in a manner precisely like that described for Serpulorbis.

Petaloconchus montereyensis, while predominantly gregarious (Plate 45, Figure 2), is represented occasionally by isolated individuals. As these individuals have been found in reproductive condition and equal in size to individuals occurring in gregarious masses, it appears there is no great dependence on communal feeding nets.

Petaloconchus montereyensis serves as host to parasites and commensals. A high rate of infection by trematode cercariae occurs in populations at Mussel Point, Pacific Grove, California. The cercariae live on the tissue of the gonad and may effectively castrate the host. Petaloconchus is also the host for a pyramidellid snail of the genus Odostomia (Chrysallida). This small parasite has been observed frequently on masses of Petaloconchus montereyensis tubes. Odostomia feeds by creeping up to the mouth of a vermetid tube and piercing the fleshy edge of the mantle tissue with its proboscis.

Amongst the masses of Petaloconchus tubes numerous other small invertebrates find refuge. Phascolosoma agassizii Keferstein, 1866 is common here; a small clam, Kellia, occurs frequently, and many other marine snails are encountered in this habitat. An almost invariable associate of P. montereyensis is the polychaete Dodecaceria fistulicola Ehlers, 1901. The calcareous tubes of this worm are generally found in a band above the zone of Petaloconchus; no clear-cut demarcation between the populations of the two species exists, and often there is a horizontal band a few centimeters wide where their tubes are intermixed. Finally, a small ostracod is often found crawling in and around the tubes of P. montereyensis. It lays its small, lens-shaped egg capsules on the center of the operculum of Petaloconchus.

Petaloconchus montereyensis may be unique among the Gastropoda in its habit of periodically producing a new operculum and moulting the old one. While marine snails have been found capable of regenerating the operculum (Hanko, 1913), I know of no other instance where total operculum replacement represents a regular activity on the part of a snail. In Petaloconchus montereyensis gross appearances suggest that most of the pedal surface has the capacity to produce opercular material. The operculum of a fully grown animal is only slightly smaller in diameter than the tube aperture. It is a flat plate with a central nucleus and bears a high, raised flange which spirals outward from the nucleus in a counter-clockwise